

GENETICAL STUDIES OF VARIEGATED PERICARP IN MAIZE¹

R. A. EMERSON
Cornell University, Ithaca, N. Y.

[Received July 24, 1916]

TABLE OF CONTENTS

	PAGE
Previous studies	1
Materials and methods, sources of error.....	2
Types of seed color and of ear color	4
Inheritance of sporophytic mutations from variegation to self color.....	9
Changes in type of variegation.....	16
Reverse mutation—self color to variegation.....	23
Suggested explanation of the inheritance of certain sporophytic variations and the non-inheritance of others.....	26
Relation of variegation to unit-factor constancy.....	29
SUMMARY	33
LITERATURE CITED	34

PREVIOUS STUDIES

Two years ago there were presented some results of a study of the inheritance of self pattern in the pericarp of maize seeds, occurring as a sporophytic² variation in variegated ears (EMERSON 1914). Further results, in entire accord with those previously reported, have now been obtained. In addition, data bearing upon new phases of the problem are also available.

The chief results reported in the earlier paper were the following: (1) The more nearly self-colored the pericarp of any seed of a variegated ear, the more likely is the progeny of that seed to produce a self-colored

¹ Paper No. 55, Department of Plant Breeding, Cornell University, Ithaca, N. Y. Most of the data here reported were obtained in connection with heredity studies conducted at the Nebraska Agricultural Experiment Station and supported by funds of that institution.

² This change has heretofore been termed somatic variation because first manifested in somatic cells. As was apparent from the start, however, the factorial modification responsible for the visible change must often occur in meristematic cells from which later arise the germ cells as well as the somatic tissues of the pericarp or even of the whole ear. Since such meristematic cells—progenitors of epidermal tissue being excluded—are germinal rather than somatic, the variation is better termed sporophytic.

ear and the less likely to produce a variegated or colorless one. (2) Self-colored ears so produced behave as if they were F_1 hybrids between self-colored and variegated or between self-colored and colorless races, depending upon whether the variegated parent ear was homozygous or heterozygous for pericarp color and upon whether it had been self- or cross-pollinated. (3) Self-colored ears also occur occasionally with the normal variegated ears in F_1 of a cross produced by pollinating a colorless race with pollen from a variegated race; and these F_1 red ears always behave in later generations as if they were hybrids between self-colored and colorless races.

As a possible interpretation of these results, I have suggested (1) that a Mendelian factor for variegation, V , is changed to a self-color factor, S , in a meristematic cell, (2) that all pericarp cells directly descended from this modified cell develop color, (3) that of the female gametes arising from such modified cells at least one-half carry the S factor in place of the V factor, and (4) that a similar factorial change is responsible for the occasional occurrence of male gametes bearing S instead of V . It was also noted in the former paper that a certain dark variegation occurring in association with a self-colored cob spot was apparently not inherited, but that, nevertheless, distinctly different types of variegation exist in an apparently homozygous condition in different strains of maize.

MATERIALS AND METHODS, SOURCES OF ERROR

Most of the data reported in my first paper were obtained from self-pollinated ears. As was there pointed out, such data are not wholly reliable for the reason that factorial changes influencing the male gametes are never detected in the staminate inflorescence. Assurance that the pollen is not carrying a factor for self color is to be had only when pollen from colorless races is employed. In all the work done since the earlier publication, therefore, seeds have been selected only from variegated ears that had been pollinated by races with colorless pericarp.

Since on the great majority of variegated ears only a few self-colored or nearly self-colored seeds occur, and since variegated ears with a considerable number of such seeds are rare, a large number of ears must be crossed in order to get a sufficient number of self-colored seeds to afford reliable indications. To hand-pollinate a sufficient number of ears for this purpose was found impracticable owing to the short period during which the work could be done and the considerable amount of time necessarily devoted to pollination in connection with other maize studies. Cross-pollination was therefore effected by detasseling all

plants grown from variegated seed and allowing them to be pollinated naturally from colorless races grown in alternate rows. The plan followed was to examine all the plants once every day and to remove all tassels as soon as they began to show above the sheaths. This work was done by careful assistants under my direction throughout the blossoming period.

In work conducted in this way, two sources of error should be noted: (1) There is a chance that a few tassels may be overlooked until after they have begun to shed pollen. (2) A few of the pollinizers may not be colorless. As to the first of these, it can be said that no open anthers were found on any tassel of the detasseled rows and that therefore, even if such occurred, the error introduced by them was probably not greater than would have resulted from the accidental entrance of foreign pollen in guarded hand-pollination.

The second source of error, on the other hand, was positively demonstrated. Of about 1000 plants in the pollinizer rows, a single plant had self red ears. Owing to the extremely unfavorable season (1913) numerous plants with fairly well developed tassels failed to produce ears. Unfortunately, therefore, it cannot be said that the single red-eared plant observed was the only one of the sort present. In fact there is reason to believe that it was not the only off-type plant present by accident, as will appear shortly. Since there was almost no chance that the colorless seeds planted could have contained any colored seeds or that such seeds were accidentally scattered in the field, it is probable that the red-eared plant was due to an accidental admixture of pollen when the parent ear was hand-pollinated the summer before.

If hand-pollination had been practiced in this investigation and pollen accidentally taken from a red-eared plant, the ears so crossed could have been discarded. In open pollination, however, it obviously could not be determined which ears had received pollen from the off-type plant. Unfortunately, I may add carelessly, the detasseled rows were harvested before the pollinizers were and consequently before the red-eared plant was discovered. It was, therefore, impossible even to discard seed ears grown near the red-eared plant.

The only method of determining how serious such accidental admixture of pollen might be was to grow progenies of colorless ears from the pollinizer rows. In order that this test might give a fair indication of the amount of off-type pollen, numerous colorless ears were taken at random from each pollinizer row and about twenty seeds from each ear were planted in 1914. In all 134 such colorless parent ears were

represented in the planting. Owing to poor germination only 1239 plants resulted. Of these one plant had self-colored ears and five had variegated ears—an error due to off-type pollen of about one half of one percent. The five variegated ears could not have come from pollen of the one red-eared plant observed, for the progeny of this plant had only self-colored and colorless ears. Pollen carrying the variegation factor must therefore have come from some other plant or plants in the pollinizer rows or from the detasseled rows. The percentage of error is so small, however, that it need occasion little difficulty.

Many of the pollinizers that were colorless with respect to pericarp had self red cobs. This fact introduces a difficulty in connection with a study of the inheritance of a peculiar form of dark variegation associated with red cob color. The matter will be considered in its appropriate place later.

TYPES OF SEED COLOR AND OF EAR COLOR

From every variegated ear used in the next season's planting, seeds of as many types of pericarp color as possible were chosen. Each type from each ear was planted separately. Almost no wholly self-colored seeds were found. In practically all cases the most nearly self-colored seeds had colorless or extremely light colored crowns. These light crowns appear as if made up of very narrow light streaks extending from part way down the side of the seeds opposite the germ up to and converging at the point of attachment of the silks to form irregular light spots (figures 1 and 2 B). Even when these grains occurred in large patches on "freak" ears, almost no wholly self-colored seeds appeared. The cob color under such "near self" seeds, whether they occurred singly or in patches of considerable size, was rarely prominently different from that of the remainder of the ear. That is, the cobs were, as a rule, variegated throughout. Under patches of near self seeds, the color of the cob was ordinarily only slightly darker than elsewhere, the change being due to a somewhat uniform development of color at the base of the glumes (figure 3 C, D).

In addition to numerous fine and often somewhat indistinct longitudinal lines of color characteristic of most variegated maize seeds, some seeds have one or more sharply defined and deeply colored stripes (figure 4). A single stripe may cover anywhere from perhaps one twenty-fifth to nine-tenths, or more, of the seed. The stripe is always self-colored, not broken by lighter variegations. Seeds in which these self-colored stripes cover from above 50 percent to 90 percent, or more,

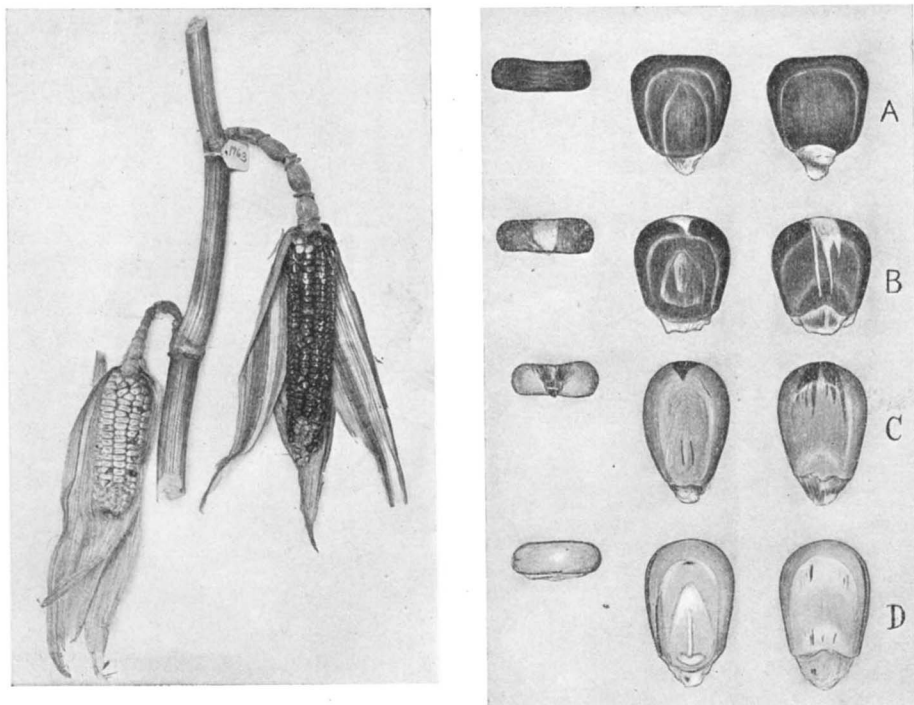


FIGURE 1.—Very light variegated type of maize with one normal ear (left) and one “freak” ear (right), the latter made up of self-colored and near self seeds except for three very light variegated ones near the shank. Note also the striped husks. From photograph by W. I. FISHER.

FIGURE 2.—Types of maize seeds, crown (left), germ side (middle), and side opposite germ (right). A, self-colored, B, near self, C, dark-crown variegated, D, very light variegated. Note the similarity in color pattern of B and C. From drawings by C. W. REDWOOD.

of the area, are classed together as “more than half self” (figure 4 B). Similarly seeds with a stripe covering from about 10 percent to somewhat less than 50 percent are designated as “less than half self” (figure 4 C).

The next most highly colored seeds are known as “dark-crown variegated.” These are usually rather evenly variegated, with dark crowns. On all sides of the seed there is usually a rather prominent light red color (brown in some strains) forming a background for the fine lines of darker color that make up the variegation. On the side of the seed opposite the germ are prominent stripes that converge at the point of attachment of the silks to form an irregular, dark crown spot (figures

2 C and 4 D). These dark-crown seeds are almost the exact reverse of the "near self" seeds described above, in that the light pattern of one is the counterpart of the dark pattern of the other. These dark-crown variegated seeds almost if not quite universally occur above a self-colored (red or brownish) spot of the cob. This is apparently equally true whether these seeds occur singly or in "freak" patches. In the latter case the exact correspondence in outline between cob and seed patches is most striking (figure 3 A, B). This is the only type of variegation that is commonly thus associated with dark color in the cob. In earlier statements (EMERSON 1913, 1914), I have spoken of an association between self-colored or near self seeds and self-colored cob spots, but I now believe that such an association is rarely if ever found.

Most variegated maize seeds lack the dark crown spot of seeds of the

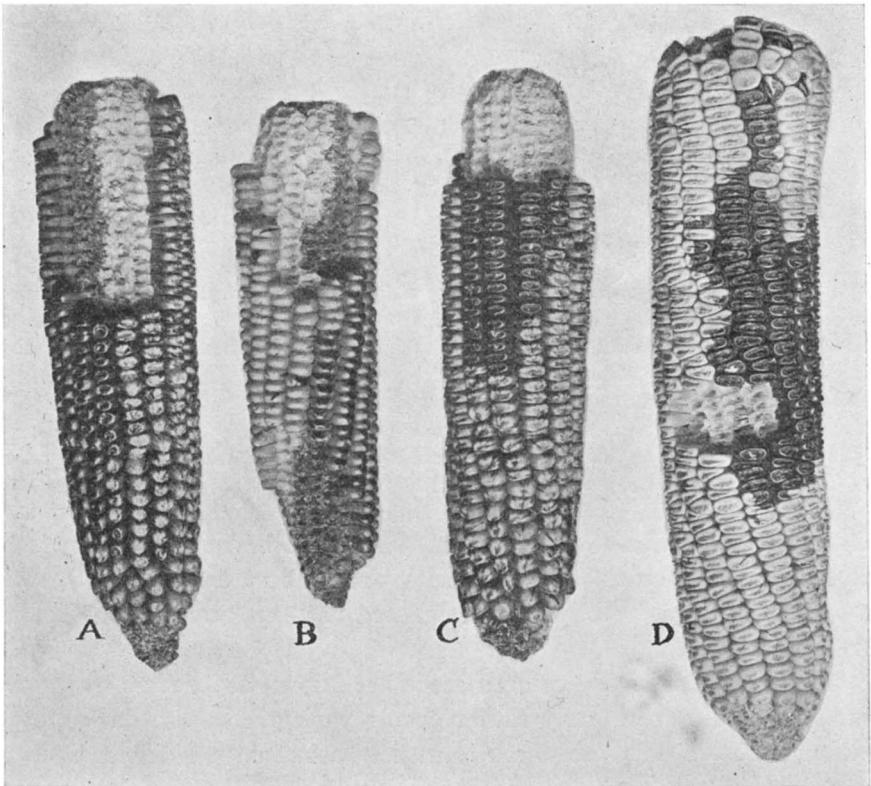


FIGURE 3.—Medium (A, C) and very light (B, D) variegated ears with "freak patches" of dark-crown (A, B) and near self (C, D) seeds. Note the association of self-colored cob spots with patches of dark-crown seeds. From photograph by W. I. FISHER.

dark-crown variegated type described above, and usually also show little or none of the light red (or brown) background noted in connection with that type. Such seeds are here known as "medium variegated" (figure 4 E). A still lighter type is distinguished as "light variegated" (figure 4 F). These differ from medium variegated seeds in degree only. They have fewer of the dark lines forming the variegation.

Still another class is known as "very light variegated." Except for occasional very narrow longitudinal lines, these seeds are almost colorless (figure 4 G). While such seeds are found occasionally on medium variegated ears, they are characteristic of certain strains of variegated maize. At a distance the ears of these strains appear colorless. Most of the seeds, however, have from one to several minute streaks or specks of color. Very light variegated ears often contain a few seeds with wholly colorless pericarp (figure 4 H).

The classes of ears are similar in part to the classes of seeds described above. Thus, I have recognized self-colored, dark, medium, light, and very light, variegated, and colorless, ears. Self-colored ears (red or brown) unlike the self and near self seeds of the variegated ears, always (so far as I have observed) have self-colored (red or brownish) cobs. In certain families a number of almost wholly self-colored ears have been observed. They are exactly like the self-colored ears in seed and cob color except that from one to at the most four or five scattered seeds are distinctly variegated. Such ears are not to be confused with the "near self" seeds described above, for their seeds, except for the very few variegated ones, are wholly self-colored. They never show the light or colorless crown spots of near self seeds. Only one ear composed almost wholly of near self seeds has ever been observed by me, and it was doubtless a "freak" ear in which the patch of near self seeds extended over nearly the whole ear instead of being confined to a smaller patch associated in the usual way with variegated grains. The ear in question not only had a light variegated cob but was borne on the same stalk with an ordinary light variegated ear (figure 1).

Ears the individual seeds of which are, throughout, say a quarter or a half self-colored, are never seen. Dark-crown variegated ears, composed wholly of dark-crown seeds, are rarely found. The three or four observed have had wholly self-colored (red) cobs. They are, I believe, to be regarded as "freak" ears, in which the patch of dark-crown seeds happened to extend over the entire ear. One such ear has been found on the same stalk with a medium variegated ear, the latter having as usual a variegated cob.

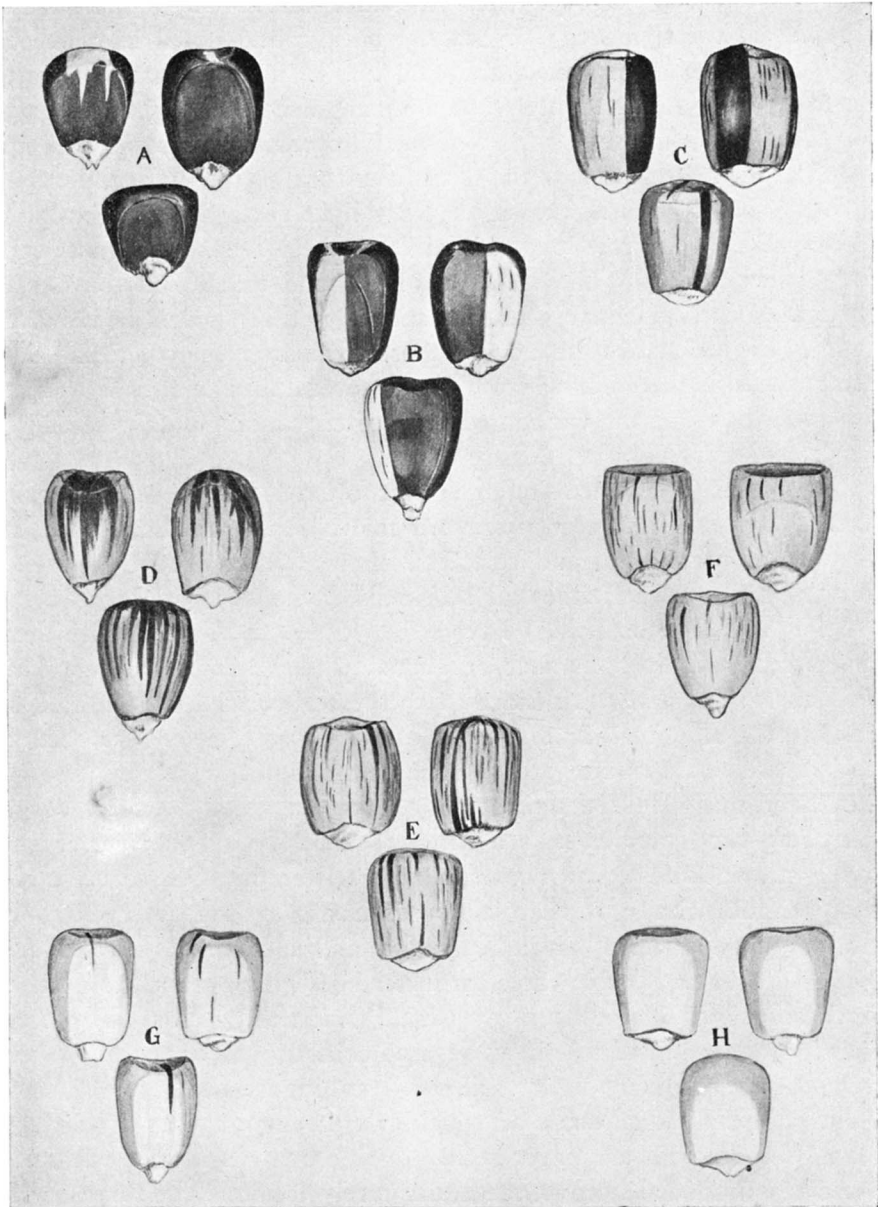


FIGURE 4.—Types of maize seeds selected from variegated ears for planting, as indicated in tables 1 and 3. A, self-colored and near self, B, more than half self, C, less than half self, D, dark-crown variegated, E, medium variegated, F, light variegated, G, very light variegated, H, colorless. From drawing by C. W. REDWOOD.

Medium variegated ears, composed in the main of medium variegated seeds but usually with scattered half self, quarter self, near self, or dark-crown seeds, and rarely freak patches of near self or dark-crown seeds, are very common (figure 3 A, C). If homozygous for variegated pericarp, they apparently always have variegated cobs. When crossed with strains having colorless pericarp and self red cobs, the resulting F_1 ears are variegated with red cobs and in F_2 all the variegated ears with red cobs are heterozygous and all with variegated cobs are homozygous for both pericarp and cob colors. Light variegated ears are like the above except that most of their grains are light variegated. Just as with medium and light variegated seeds, no sharp line of demarkation exists between medium and light variegated ears. While some ears are clearly much lighter than others, numerous intermediates are usually found in the same lots.

Very light variegated ears are composed mostly of very light variegated and colorless seeds. They rarely produce self-colored, near self, or dark-crown seeds, and I have observed among them only a few "freak" ears with large patches of dark-crown or near self seeds (figure 3 B, D). In this respect they differ notably from medium variegated ears. Their cobs are very light variegated or nearly colorless, except, as in the case of medium variegated ears, when they have been crossed with colorless-seeded, red-cobbed types, in which case all heterozygous ears have red cobs. Some apparently wholly colorless ears have been observed in strains of very light variegated maize and are doubtless to be regarded as an extreme expression of this type of variegation. Self-pollinated seeds of one such ear were found to yield a progeny consisting mainly of very light variegated ears. Very light variegation is recessive to medium variegation, as will be shown later, and the two types segregate rather sharply in F_2 .

INHERITANCE OF SPOROPHYTIC MUTATIONS FROM VARIEGATION TO SELF COLOR

The variegated ears, cross-pollinated by plants with colorless pericarp, as noted earlier in this paper, may be divided into two general lots, one of which was homozygous with respect to pericarp color and the other of which was heterozygous from having been crossed with colorless maize the previous generation. A part of the homozygous variegated lot was in reality heterozygous for medium and very light variegation.

Of the lot that was heterozygous for variegated pericarp, seeds of various color types were selected from seventy-five parent ears, and

progenies totaling 1140 plants were grown. Since we are here concerned with the inheritance of self color as contrasted with variegation, all the variegated ears will be lumped together without respect to the type of variegation. The numbers of self-colored, variegated, and colorless ears produced by the various types of seeds are given in table 1.

Since the parent ears were heterozygous for pericarp color and were cross-pollinated by colorless maize, fifty percent of the progeny of each class of seeds should have been colorless. The percentages of plants with colorless ears actually observed ranged from a little less than 46 to a little over 62. The percentage of colorless ears in the lot as a whole was 50.96. It seems likely that the individual deviations from the expected 50 percent are without significance. There is certainly no regular tendency toward either an increase or a decrease in the percentage of colorless ears from the self-colored seed to the lighter variegated seed. It can be concluded therefore that these data afford no evidence of any effect of the amount of color in the seeds of heterozygous variegated ears upon the relative numbers of colored and colorless offspring.

The things that stand out most prominently in these results are, (1) the direct relation between the amount of self color in the seeds planted and the percentage of plants with self-colored ears in the progenies in the first three classes; (2) the lack of any such relation between the amount of color in the seeds and the percentage of self-colored ears produced from the various classes of variegated seeds; and (3) the entire absence of variegated ears in the progeny of self-colored and near self seeds.

It seems likely that the difference in percentages of self-colored ears from the several classes of variegated seeds is without significance. Only a single self-colored ear appeared in the progeny of any one class of these seeds. It is perhaps, however, significant that no regular increase in self-colored ears appears as we pass from the very light variegated seeds with very little color, to the dark-crown variegated seeds which have considerable color, particularly at the crown. The possible significance of this fact will be considered later.

The percentages of self-colored ears in the plants grown from self or near self seeds, from more than half self seeds, from less than half self seeds, from variegated seeds (all classes of the latter being lumped together), and from colorless seeds, approximately 51.1, 27.5, 6.9, 0.3 and 0, respectively, are similar to the percentages calculated from results previously reported (EMERSON 1914). The combined results, including all data now available, are brought together in table 2.

TABLE I
Progenies of different classes of maize seeds from seventy-five heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants			Percentages			
	Self-colored ears	Variegated ears	Colorless ears	Total	Self-colored ears	Variegated ears	Colorless ears
Self and near self.....	23	—	22	45	51.11	—	48.89
More than half self.....	14	5	32	51	27.45	9.81	62.74
Less than half self.....	6	38	43	87	6.90	43.68	49.42
Dark-crown variegated.....	—	91	78	169	—	53.85	46.15
Medium variegated.....	1	159	209	369	.27	43.09	56.64
Light variegated.....	1	48	41	90	1.11	53.33	45.56
Very light variegated.....	1	141	125	267	.37	52.81	46.82
Colorless	—	31	31	62	—	50.00	50.00
Total	559	581	1140	49.04	50.96		

TABLE 2
Progenies of different classes of maize seeds from heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants				Percentages		
	Self-colored ears	Variegated ears	Colorless ears	Total	Self-colored ears	Variegated ears	Colorless ears
Self and near self.....	37	—	36	73	50.68	—	49.32
More than half self.....	18	7	34	59	30.51	11.86	57.63
Less than half self.....	9	43	52	104	8.05	41.35	50.00
Variegated	10	704	754	1468	.68	47.96	51.36
Colorless	—	58	51	109	—	53.21	46.79
Total	886		927	1813		48.87	51.13

That the percentage of self-colored ears in the progeny is roughly proportional to the amount of self color in the seeds planted is evident. Since the parent ears were heterozygous for variegated pericarp, the V factor was simplex. On the basis of the hypothesis advanced in my former paper, if this single V factor is changed to an S factor early enough so that the whole pericarp is self-colored, the gamete concerned is assumed always to arise from a modified cell containing S instead of V . Since V , from which S came, was simplex, S will also be simplex. Half the gametes formed in connection with self-colored seeds will, therefore, carry S and half will carry a factor for colorless pericarp, so that half the plants resulting from such self-colored seeds should have self-colored ears and half colorless ears. This expectation has been almost exactly realized.

If the seeds that are classed here as more than half self-colored are assumed to average 75 percent self and those classed as less than half self-colored are assumed to average 25 percent self, the percentages of plants with self-colored ears expected from them are 37.5 and 12.5 respectively. The percentages actually observed were 30.51 and 8.65 respectively, a sufficiently close approximation to expectation when allowance is made for the fact that the seeds planted may not have averaged 75 percent and 25 percent as assumed.

Perhaps the most striking feature of these results is the total lack of variegated ears in the progeny of self and near self seeds. This is in exact accord with expectation, since if a simplex V mutates to an S , V could be present in no gamete associated with a self-colored seed. The number of plants from self-colored seeds in table 2 is small, to be sure, totaling only 73. It is permissible, however, to add to this number the records of HARTLEY (1902), of EAST and HAYES (1911, pp. 106-107) and of my own open-pollinated cultures (EMERSON 1914), since the parent ears in all these cases were obviously heterozygous for variegated pericarp and were presumably pollinated from colorless plants. Combining all these lots, we have from self and near self seeds 186 plants with self-colored ears, 177 with colorless ears, and not a single plant with variegated ears.

A noteworthy point in connection with this result is that many, doubtless most, of the seeds planted were not wholly self-colored but were what are here called near self, that is, they had a small colorless or nearly colorless spot at the crown. It will be recalled that the dark-crown variegated seeds (table 1) produced no self-colored ears though they are characterized by dark colored crowns corresponding almost exactly

to the light crowns of the near self seeds. It would appear, therefore, that there is no connection between the color at the crown of the seed and the production of self-colored ears in the next generation.

We have now to consider the behavior of variously colored seeds from homozygous variegated parent ears. All these ears were cross-pollinated by colorless maize just as were the heterozygous ears considered heretofore. Seeds of various color types were selected from 80 homozygous variegated ears and a total of 1972 plants grown from them. The results are recorded in table 3.

TABLE 3

Progenies of different classes of maize seeds from eighty homozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies				
	Number of plants			Percentages	
	Self-colored ears	Variegated ears	Total	Self-colored ears	Variegated ears
Self and near self.....	71	72	143	49.65	50.35
More than half self....	43	67	110	39.09	60.91
Less than half self....	16	150	166	9.64	90.36
Dark-crown variegated..	1	528	529	.19	99.81
Medium variegated.....	2	607	609	.33	99.67
Light variegated.....	2	125	127	1.57	98.43
Very light variegated...	1	269	270	.37	99.63
Colorless	—	18	18	—	100.00

Here, just as with the heterozygous variegated parent ears, the several classes of variegated seeds showed no regular difference as to the percentage of self-colored ears produced. The considerable amount of color at the crown of dark-crown variegated seeds, as noted before, has no apparent relation to the production of self-colored ears in the progeny.

The percentages of plants with self-colored ears from the five classes of seeds—self or near self, more than half self, less than half self, variegated (all classes together), and colorless—are not far different from the percentages found in case of heterozygous parent ears, as can be seen from the following comparison (table 4).

The important point here is that, when the variegation factor is duplex, the percentage of self-colored ears in the offspring is not greater than when that factor is simplex. This indicates that ordinarily only one

TABLE 4

Self-colored ears in progenies of different classes of seeds from homozygous and heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Percentage of self-colored ears	
	Homozygous parents	Heterozygous parents
Self and near self.....	49.65	50.68
More than half self.....	39.09	30.51
Less than half self.....	9.64	8.65
Variegated39	.68
Colorless	0	0

of the duplex factors of a sporophytic cell mutates. That is, VV becomes VS not SS . Both V factors may at times change to S factors, but such is not the case frequently enough to affect materially the percentage of self-colored ears and no test other than percentage differences is available. This question has been discussed elsewhere (EMERSON 1913).

Since only one of the duplex V factors ordinarily changes to an S factor in any one sporophytic cell, and if one V factor mutates as readily as the other, it follows that on the average about twice as many self-colored seeds should be found on homozygous as on heterozygous variegated ears. The same difference should be noted in the progenies of non-colored maize when cross-pollinated by homozygous and heterozygous variegated-eared plants. Attention is being given to this matter at the present time.

As noted earlier in this discussion, some of the ears classed above as homozygous were in reality the result of a cross of two distinct strains of variegated maize, one medium variegated and the other very light variegated. While there is some variation in both of these strains, particularly in the medium variegated one, some ears having more color than others, there is no overlapping between them. Ears of the very light variegated strain often appear colorless until examined somewhat closely. A single cross between this strain and a self-colored strain gave sharp segregation in F_2 into self-colored and very light variegated ears with none medium variegated. Numerous crosses of medium variegated with self-colored strains have likewise thrown self-colored and medium variegated offspring with no very light variegated ears. Self color is dominant to both types of variegation. Finally, crosses between the two

variegated strains have shown medium variegation to be dominant to very light variegation in F_1 and have resulted in simple Mendelian segregation in F_2 .

Both medium variegated and very light variegated strains have occasional seeds that are self-colored, near self, half self, etc., though this is much less common in the very light variegated strain than in the medium variegated one. The F_1 medium variegated ears from the cross of the two strains also, of course, have some such seeds. A study of the progeny of the several classes of seeds from thirty of these F_1 variegated ears, a total of 747 plants, has given important results of a kind not heretofore reported. They are brought together in table 5.

The important features of these records are: (1) The percentage of plants with very light variegated ears was not greater when the seeds planted were very light variegated than when they were medium and dark-crown variegated. From all classes of variegated seeds together, approximately 49 percent of the offspring were medium variegated and 51 percent very light variegated, where 50 percent of each was to have been expected. (2) The percentage of self-colored ears was roughly proportional to the amount of self color in the seeds planted. The deficiency of self-colored ears below the expected 50 percent from near self seeds is probably without significance, being due most likely to the small numbers involved. (3) The percentage of medium variegated ears decreased as the percentage of self-colored ones increased. Evidently, the self-colored ears were produced at the expense of medium variegated ears and not at the expense of very light variegated ones.

The significance of this is that in these F_1 plants the factor for medium variegation mutates much more frequently than the factor for very light variegation,— V_mV_i ordinarily becomes SV_i rather than V_mS . This is to be expected from the fact that self-colored and near self seeds occur much less frequently on very light variegated ears than on medium variegated ones. Whether V_mV_i ever becomes V_mS cannot now be said for no evidence is available. This probably does occur, however, for there is abundant evidence that V_iV_i does occasionally, though rarely, become V_iS .

CHANGES IN TYPE OF VARIEGATION

Both medium and very light variegated ears of maize are quite as likely to exhibit pronounced sporophytic variations to dark-crown variegation as to self color. The dark crown spots of these seeds make a "freak patch," or even a single seed, to stand out from the normally

TABLE 5
Progenies of different classes of seeds from thirty F₁ variegated ears of a cross between medium variegated and very light variegated strains, pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants			Total	Percentages		
	Self-colored ears	Medium variegated ears	Very light variegated ears		Self-colored ears	Medium variegated ears	Very light variegated ears
Self and near self.....	16	—	27	43	37.21	—	62.79
More than half self.....	16	7	31	54	29.63	12.96	57.41
Less than half self.....	8	25	35	68	11.76	36.77	51.47
Dark-crown variegated.....	—	92	108	200	—	46.00	54.00
Medium variegated.....	—	102	104	206	—	49.51	50.49
Very light variegated.....	—	91	85	176	—	51.70	48.30
Total.....	40	317	390	747	5.35	42.44	52.21

colored seeds of the same ear almost as strikingly as does a patch of near self seeds. The fact that dark-crown variegated seeds are almost if not quite universally underlaid by a self-colored cob patch corresponding accurately in outline to the patch of seeds with dark crowns adds not a little to the distinctiveness of this sporophytic variation (figure 3 A, B). In my first paper (EMERSON 1914), it was noted that there was then *no evidence of the inheritance of this variation*. The same statement might suffice even at present, but the evidence against such inheritance is now so strong that it seems important to present it here, if for no other reason than to emphasize a surprising difference between two almost equally striking sporophytic variations that often occur on the same ear.

Occasionally an ear is found to be divided sharply into two parts, one consisting of seeds that show the ordinary medium-variegation pattern and the other of seeds that are light variegated. Such variations have been much less common in my material than the occurrence of dark-crown variegated and near self seeds. In addition to these very distinct variations, many medium variegated ears have some grains showing all gradations from medium to light or very light variegation.

Of all the instances of sporophytic change in type of variegation that I have investigated, only a few afford any indication of having reached the germ plasm. All these occurred in a single lot of maize. A medium variegated ear with variegated cob, cross-pollinated by a strain of maize with colorless grains and self-colored cobs, produced both medium variegated and very light variegated offspring, all, of course, with self-colored cobs. The parent was, therefore, heterozygous for the two types of variegation. Since it was pollinated by colorless maize, both types of offspring must have been heterozygous, the one for medium variegation and the other for very light variegation. If V_m and V_l are allelomorphs, as there is every reason to believe, no ear could have contained both of these factors. An ear of this lot with medium variegated grains and red cob was self-pollinated and next generation gave colorless ears with self-colored cobs, medium variegated ears with self-colored cobs, and medium variegated ears with variegated cobs, in a ratio approximating 1 : 2 : 1, as was expected of it. No light variegated ears were noted and, of course, none were expected. Since self color of cob is allelomorphous to variegated color of grains, the ears with self-colored cobs were obviously heterozygous for pericarp color as well as for cob color and those with variegated cobs were homozygous. The latter may, therefore, be designated as V_mV_m . Three of these homozygous medium

variegated ears had more or less distinct "freak" patches of rather light variegated seeds. The two classes of seeds from these three ears were planted separately with the following results (table 6).

TABLE 6

Progenies of medium variegated and light variegated seeds of homozygous medium variegated parent ears cross-pollinated by colorless maize.

Seeds planted	Number of plants		
	Medium variegated ears	Light variegated ears	Very light variegated ears
Medium variegated	64	12	0
Light variegated	41	10	18

The ears recorded as medium variegated and light variegated respectively were not sharply separable on account of numerous intermediates and should possibly have been classed together. The very light variegated ears, on the other hand, were a fairly uniform lot and were distinctly lighter than the lightest of the ears classed as light variegated. The striking feature of these records is the fact that no very light variegated ears were produced from medium variegated seeds, while from the light variegated seeds of the same parent ears there were 18 plants, about 26 percent of the total number, with very light variegated ears.

Upon the behavior of such very light variegated ears in later generations will depend the answer to the question whether they are true mutations. Until such tests can be made, it is perhaps idle to speculate about the possible manner of their origin. There are two features of the result, however, that deserve comment. We know that the parent ears were V_mV_m and that they were pollinated by colorless maize. If it be assumed that the very light variegated ears arose through a change of V_m to V_v —the only assumption that seems at all reasonable,—how can we explain the visible somatic modification, and how account for the fact that only about 26 percent rather than 50 percent of the ears from the light colored seeds were very light variegated?

If V_mV_m change to V_vV_v , the seeds should be very light variegated, but in that case 100 percent of the progeny should be very light variegated. If V_mV_m becomes V_mV_v , 50 percent of the offspring should be very light variegated but the parent seeds themselves should not have been affected,

since medium variegation has been found to be dominant to very light variegation. As a matter of fact my descriptions, made, of course, the year before these results were obtained, indicate that the parent seeds were not what I have termed very light variegated, but were merely sufficiently lighter than the medium variegated seeds of the same ears to be readily detected when found in solid patches on those ears. Perhaps medium variegation is not always completely dominant over very light variegation. This, however, since I have not noted partial dominance in actual crosses between these types, is so obviously an attempt to make the facts fit the hypothesis that the matter had best be dismissed with the mere statement that the record presented here is the only evidence, slight as it is, that a sporophytic change in type of variegation of maize pericarp is ever of the nature of a true mutation.

From various other ears both homozygous and heterozygous for medium variegated pericarp, light and very light variegated seeds scattered over the ears have been selected and have given no evidence of the inheritance of the type of variegation shown by them. The available data are given in table 7. The records are grouped so that parent ears of like nature, homozygotes or heterozygotes, are classed together.

From many of the same parent ears employed for the comparison given in table 7 and from some others, ninety-one in all, dark-crown variegated seeds were selected for planting in comparison with medium variegated seeds of the same ears. The data obtained from these tests are given in table 8.

It is obvious that, so far as the available data go, they give no indication that dark-crown variegation occurring as a sporophytic variation is ever inherited. This behavior is noteworthy in contrast to the definite inheritance of self or near self color when it occurs as a sporophytic variation in variegated maize—the more particularly so because the visible change is quite as definite and almost as striking in the one case as in the other. The cause of this difference is reserved for discussion later in this paper.

The possible inheritance of self color of the cob, which occurs as a sporophytic variation, so far as I have observed, universally associated with dark-crown variegated seeds on otherwise variegated cobs, is of even more interest than the inheritance of variations in pericarp color. Dark-crown variegation of maize seeds does not, so far as I am aware, exist except as a sporophytic variation, while self color of the cob is always associated with the more common self colors of the pericarp,

TABLE 7
Progenies of light variegated and of medium variegated seeds from seventy-two homozygous and heterozygous variegated ears.

Seeds planted	Progenies						
	Number of plants					Percentage	
	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total	Light variegated ears	Very light variegated ears
Twenty-one ears— Medium variegated.... Light to very light variegated	118	7	—	—	125	5.60	—
Twenty-four ears— Medium variegated.... Light to very light variegated	111	6	—	—	117	5.13	—
Twenty-seven ears— Medium variegated.... Light to very light variegated	82	8	—	98	188	4.26	—
Twenty-seven ears— Medium variegated.... Light to very light variegated	27	3	—	24	54	5.56	—
Twenty-seven ears— Medium variegated.... Light to very light variegated	122	8	167	—	297	2.70	56.23
Twenty-seven ears— Medium variegated.... Light to very light variegated	44	4	49	—	97	4.12	50.52

TABLE 8
Progenies of dark-crown variegated and of medium variegated seeds from ninety-one homozygous and heterozygous variegated ears.

Seeds planted	Progenies						Percentage		
	Number of plants						Dark-crown variegated ears	Light variegated ears	Very light variegated ears
	Dark-crown variegated ears	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total			
Twenty-seven ears— Medium variegated....	—	243	9	—	—	252	—	3.57	—
Dark-crown variegated	—	200	1	—	1	202	—	.50	—
Thirty-seven ears— Medium variegated....	—	76	9	—	114	199	—	4.52	—
Dark-crown variegated	—	64	4	2	60	130	—	3.08	1.54
Twenty-seven ears— Medium variegated....	1	134	9	141	—	285	.35	3.16	49.47
Dark-crown variegated	—	70	3	91	—	164	—	1.83	55.49

dark red and dark brown, and is frequently found in strains with colorless pericarp.

Unfortunately, the occurrence of self-colored cobs in the progeny of dark-crown variegated seeds cannot in these studies be taken as an indication of the inheritance of a sporophytic variation in cob color, for the reason that a considerable number of the plants used as pollinizers, though colorless as regards pericarp, had self-colored cobs. A part of the progeny of all seed classes was, therefore, expected to have self-colored cobs, so that the only criterion of the inheritance of sporophytic variation to self color in cobs is the relative percentages of plants with self-colored cobs in the progenies of dark-crown variegated and of medium variegated seeds.

Of the 1057 plants with variegated ears listed in table 8, 435 came from dark-crown seeds all of which were associated definitely with self-colored patches of the otherwise variegated cobs to which they were attached, while 622 grew from medium variegated seeds associated with variegated cob patches of the same ears. All these plants with variegated ears had variegated cobs except 60 of those from dark-crown seeds and 88 of those from medium variegated seeds. The percentages of plants with self-colored cobs were, therefore, about 13.8 for the progeny of dark-crown seeds and about 14.2 for the progeny of medium variegated seeds. Of 1486 plants grown from seed of the plants with colorless pericarp and colorless cobs used as pollinizers, 208, or almost exactly 14 percent, had self-colored cobs. There is certainly nothing in these results to indicate that a sporophytic variation from variegation to self color of the cob is inherited.

REVERSE MUTATION—SELF COLOR TO VARIEGATION

In certain cultures of maize there have been noted ears that are self-colored except for a single variegated grain or a grain that is half variegated and half self, one-third variegated and two-thirds self, etc. Frequently, two or three and in a few cases as many as five such grains have been found on a single otherwise wholly self-colored ear. In the records presented earlier in this paper all such ears have been listed as self-colored, and I think rightly so, just as ears that were variegated throughout except for a few self-colored seeds have been listed as variegated. In short, I regard the occurrence of these variegated seeds on self-colored ears as due to sporophytic mutations from self color to variegation. I must admit, however, that there is at present very little direct evidence as to the real nature of these variegated seeds.

Few such variegated seeds have been tested and most of these have not been wholly desirable material for the tests. The seeds tested were found mainly on ears that were heterozygous for self-colored and variegated pericarp, SV . Even the self-colored seeds of these ears should throw 25 percent or 50 percent variegated ears the next generation, the actual percent depending, of course, upon whether the parent ear was self-pollinated or crossed by colorless maize. If the S factor of such an ear change to V the result would be to produce homozygous VV tissue. Any seed in the modified part of the ear would be variegated. But collectively such seeds would produce only 50 percent of variegated offspring if self-pollinated, because half the pollen would carry dominant S , and 100 percent variegated if crossed by colorless maize. The only criterion of the assumed mutation is, therefore, a difference in percentages of variegated offspring from the self-colored and variegated seeds of the same ear. This would be fairly conclusive if larger numbers could be dealt with, but since the numbers that can be grown are small owing to the rarity of such variegated seeds, the results are not satisfactory.

Self-colored ears that are heterozygous for self-colored and colorless pericarp afford satisfactory material but as yet I have been unable to take full advantage of it. Half the gametes of such a plant ordinarily carry the S factor and the other half carry a factor for colorless pericarp. If then S become V in connection with variegated grains and if the ear were cross-pollinated by colorless maize, the variegated seeds should throw 50 percent variegated and 50 percent colorless offspring while the self-colored seeds should throw 50 percent self-colored and 50 percent colorless offspring. The failure of self-colored seeds to produce variegated ears and of variegated seeds to produce self-colored ears would furnish definite evidence of a factorial change. Large numbers would not, therefore, be required.

If, on the other hand, this self-colored ear, heterozygous for pericarp color, were self-pollinated, the self-colored seeds would, of course, throw 75 percent self-colored and 25 percent colorless ears, while the variegated seeds of the same parent ear would produce 50 percent self, 25 percent colorless and 25 percent variegated. But here comparison of ratios is not necessary—the mere presence of variegated ears, barring accidental pollination, is evidence of the factorial change from S to V . From a few variegated and partly variegated seeds from self-pollinated parent ears, all the expected classes of ears—self, colorless, and variegated—have been obtained. Only a single variegated ear, however, has been

produced from the few variegated seeds tested. This ear was self-pollinated and threw only variegated and colorless offspring, just as was expected on the basis of the assumed factorial change. But the same result would necessarily have followed if the variegated ear in question had been produced through the action of a stray grain of pollen carrying V on a seed that might otherwise have produced a colorless ear. While the chance is rather small that such a stray grain of pollen might have happened to fertilize one of the very few variegated seeds of the parent ear rather than one of the numerous self-colored seeds, the possibility is not excluded. No adequate evidence, therefore, of a factorial change from S to V is available. It can merely be said that such a change is strongly suggested. The assumption of factorial change is strengthened by the fact that the variegated ears of this lot are more fully colored than those of any other variegated strain in my collection. The few ears observed have more seeds near self, half self, etc., than other strains and more color on the variegated seeds. Moreover, this tendency has persisted to the second generation.

It is of interest to note the fact that in some lots of self-colored maize, which have arisen by sporophytic mutation from variegated strains, no variegated or partially variegated seeds have ever been observed. In other lots, on the contrary, the tendency is very strong to produce a few variegated seeds on the otherwise self-colored ears. In most of these cultures from one-third to two-thirds of the self-colored ears have a few variegated grains. It seems particularly noteworthy that the only cultures to show this apparent reverse mutation trace back to one or the other of two ears of maize obtained some years ago. Some lines of self-colored maize originating from these same two ears have, on the other hand, never shown a tendency to produce variegated seeds.

From all this it seems likely that, if the sporophytic variation here under consideration is a reversal of the common mutation which goes from V to S , there are differences between the S factor of different strains in respect to the frequency with which it may change to a V factor just as there are different sorts of V factors, one of which, V_m , mutates more readily than another, V_i . The possibility, however, that the difference may not be inherent in the S or V factors themselves, but may be due to some interaction of other factors with the S or V factor in certain strains is not precluded.

Another point of no little interest is the fact that up to the present time no variegated seeds have been found on ears known to be homozygous for self color, SS , though they have appeared frequently in re-

lated heterozygous families, in which S was simplex and associated with simplex V or with a factor for colorless pericarp. This, if found to hold when further results have been obtained, will have a bearing upon the question of whether both of the duplex factors ever mutate at the same time (see EMERSON 1913). It has been shown earlier in this paper that as a rule only one of the duplex factors VV mutates, thus giving rise to SV rather than SS . Owing to the dominance of S over V , a mutation of S to V affecting only one of the duplex factors in homozygous self-colored maize, would not be visible as a somatic variation, for VS could not be distinguished from SS .

SUGGESTED EXPLANATION OF THE INHERITANCE OF CERTAIN SPOROPHYTIC VARIATIONS AND THE NON-INHERITANCE OF OTHERS

In this and earlier papers, it has been shown that a sporophytic variation from variegation to near self color of the pericarp of maize is definitely inherited, while quite as striking a variation from light and medium variegation to dark-crown variegation of the pericarp is never inherited. The contrast is particularly noteworthy because the non-inherited dark-crown variegation is apparently always associated with a change in cob color from variegation to self pattern, this change also being non-inherited, while the inherited near self variation of the seed is accompanied by only a slight change in cob color, though the self-colored ears produced by such seeds always have self-colored cobs.

When the difference in behavior was first recognized, it seemed possible that it might be related in some way to the stages in ontogeny at which the sporophytic variations in question arise. It was assumed that the modification to self color takes place previous to the differentiation of the megaspore mother cell and in the direct line of its cell ancestry. On the other hand, the fact that much color develops only near the crown of the seeds of the non-inherited dark-crown variation suggested that this modification might occur late in the development of the pericarp and, therefore, in a line of cell generations collateral to that from which the germ cell arises, rather than in direct line with it. A notable difficulty with any such hypothesis is that a factorial change occurring late in the development of the pericarp could hardly be supposed to influence the color of the underlying cob so that every dark-crown seed would be associated with a self-colored cob spot. Moreover, to account for large patches of near self seeds, it had to be assumed that the factor change might sometimes take place almost simultaneously in the rudiments of every grain so that the grains become self-colored

while the cob remains variegated (EMERSON 1914). The universal appearance of self-colored cobs with self-colored seeds in the progeny of these near self seeds led naturally to subsidiary hypotheses concerning the simultaneous modification of factors for cob and pericarp color (EMERSON 1913).

If further investigation confirms the indications already at hand, all these facts can be harmonized and explained on a simple histological basis, which will render at least some of the hypotheses unnecessary and unwarranted. Microscopic sections of mature seeds made for me by Mr. E. W. LINDSTROM, graduate student in genetics at CORNELL UNIVERSITY, indicate plainly that the outer epidermal layer of cells of the pericarp of near self seeds is without color while the underlying part of the pericarp, except at the crown of the seeds, is largely, if not wholly colored. In contrast to this condition, the dark-crown seeds certainly have color in the outer epidermis of the pericarp and, except at the crown, lack color in much of the underlying part of the pericarp. The sections also show indisputably that there is some deep-lying color even at the sides of these dark-crown grains, but whether this color is confined to epidermal cells has not been determined. According to TRUE (1893), the integuments of the ovule, which are mostly two cells thick and therefore probably mostly epidermal, largely disintegrate as the seed develops, but the thick-walled cells of the inner epidermis of the pericarp remain intact. There is also a possibility that the epidermis of the nucellus may have contributed slightly to the color observed in sections of dark-crown seeds. Wholly self-colored seeds of plants produced from the near self variation apparently have color in both the epidermal and the sub-epidermal cells of the pericarp.

Sections of very young maize ears furnished me by Mr. E. G. ANDERSON, graduate student in genetics at CORNELL UNIVERSITY, show the glumes to have only two layers of cells, except near the base where they are several cells in thickness. From this I infer that even the mature glumes are largely epidermal in origin. If this be true, the dark-crown variation, in which the color is now suspected of being confined to the epidermal layers, would necessarily be associated with self-colored cob spots, while the near self seeds, with presumably no color in epidermal tissue would be associated with glumes that were non-colored, except at their thick bases. The wholly self-colored seeds produced in the next generation by near self seeds should, of course, have self-colored cobs because here there is color in the epidermis as well as in the sub-epidermal cells.

There yet remain to be explained the light crown spot of near self seeds, the exactly corresponding dark crown spot of dark-crown variegated seeds, and the lack of color differentiation at the crown of seeds of self-colored ears produced by near self seeds. While the matter can be settled definitely only by a study of the developing seeds, there are some reasons for the belief that the crowns of maize seeds are largely epidermal in origin. The exact correspondence in pattern between the colored lines converging at the point of attachment of the silk of dark-crown grains and the light spot of near self seeds has been noted repeatedly. So far as I have observed self-colored seeds occurring individually or in small groups within a large "freak" patch of dark-crown seeds and self-colored cob always lack the light crown spot. Likewise, in a large patch of near self seeds with variegated cob, there sometimes occur small patches of self-colored cob and, so far as observed, the seeds of the small patches are wholly self-colored, lacking the light crown spots.

All of these peculiarities of coloration of seeds and cobs are thus readily harmonized, if it turns out on further study that the color of the dark-crown variation is limited to epidermal tissue and the color of the near self variation to sub-epidermal tissue. And, more important still, no other explanation of the non-inheritance of the one type and the inheritance of the other is needed. Sporophytic changes occurring in epidermal cells can, of course, have no influence upon the germ cells which arise from sub-epidermal tissue. Modifications of genetic factors in epidermal cells are doubtless not fundamentally different from such changes in sub-epidermal cells, but if the inheritance of a variation is to remain the criterion of mutation, mere epidermal variations must be regarded at most as nothing more than potential mutations.

In various papers (EMERSON 1911, 1913, 1914), it has been assumed that factors for colors or color patterns of the pericarp are distinct from similar factors of the cob glumes and that these glume and pericarp factors are closely linked. These assumptions were made to account for such observations as the following. When a race having color in both glumes and pericarp is crossed with one lacking color in these parts, no new combinations of glume and pericarp color are produced. When a race having self-colored cob glumes and colorless pericarp is crossed with one having colored pericarp and colorless or nearly colorless glumes, F_1 has color in both glumes and pericarp, but produces no gametes bearing factors for this combination of colors, so that in F_2 there appear only the parental and F_1 combinations, never colorless glumes with colorless pericarp. It was natural to suppose that also in case of variegated peri-

carp and cob glumes separate factors were concerned, namely, V_p , and V_c . To account for the appearance of self-colored cobs with self-colored seeds in the next generation from near self seeds occurring as somatic variations on otherwise variegated ears, it seemed necessary to assume a simultaneous modification of V_p and V_c to S_p and S_c . And this occurrence it was suggested might be due to the close association of V_p and V_c in the chromosomes.

The histological explanation suggested above, of the inheritance of certain, and the non-inheritance of other, sporophytic variations, if found to be correct, will make it seem more likely that the self color and variegation factors responsible for the color patterns of the pericarp are the identical factors concerned with the same color patterns in the glumes. Attention has already been called by MORGAN *et al.* (1915) to the possibility that I have been dealing with cases of multiple allelomorphs rather than with closely linked factors. In the light of the present study MORGAN'S view seems the more reasonable one.

If the explanation here suggested for the inheritance of certain sporophytic variations in maize and the non-inheritance of others is found to be the true one, it will be of interest to investigate similar situations in other plants. It will be remembered that DE VRIES (1905, pp. 309-328) reported the inheritance of a sporophytic change from variegated to self red flower color in *Antirrhinum*, while CORRENS (1910) described a similar variation in *Mirabilis* flowers, that is not inherited. I have previously suggested (EMERSON 1914) that these cases may be similar to the inherited and non-inherited sporophytic variations in maize. At present there is nothing more than this resemblance in behavior to suggest a similar explanation, but it is proposed to investigate the situation in these and other variegated flowers.

RELATION OF VARIEGATION TO UNIT-FACTOR CONSTANCY

If the results here recorded have been correctly interpreted, they have an important bearing upon the question of unit-factor constancy. Self-color arises from variegation and is then inherited as a simple allelomorph to variegation. It follows, therefore, that a unit factor concerned in the development of variegated pericarp is occasionally changed to a factor concerned in the development of self color. Moreover, the same change—or a change that produces the same end result—occurs repeatedly. There is some evidence also that a factor for self color thus produced may, by a reverse mutation, become again a factor for variegation.

The variegation and self-color factors belong to a series of not less than nine or ten multiple allelomorphs which include self red and self orange, white-capped red, basal red, and colorless pericarp, associated with either self red or white cobs, and at least three types of variegated pericarp associated with similarly variegated cobs. The fact that such a series of multiple allelomorphs exists is evidence that a fundamental factor concerned in the development of pericarp and cob colors and color patterns has at one time or another mutated in diverse ways. That these several factors are distinct, not merely with respect to the end results which they help to produce as exhibited in types of coloration of mature ears, but also as regards the relative frequency with which they are now mutating, is obvious to anyone who has worked with ear colors of maize. Only two instances of sporophytic changes from self red to white—or perhaps they were from white to red—have been observed by me. Both of these variations were accompanied by modifications of the fundamental color factor concerned (EMERSON 1914). I have also found two ears with both self red and self orange, or brownish orange, seeds in separate patches. There is some scarcely conclusive evidence that in these cases also factorial modifications were responsible for the somatic variations observed. In no other instances, not involving variegation, have such changes been noted. When it is remembered that large numbers of individuals of these types have been studied in pure strains and in crosses, the rarity of such factorial changes becomes evident.

There is some evidence that a self-color factor, that has arisen by mutation from a variegation factor, may, by a reverse mutation, become a variegation factor. The change is comparatively infrequent, not more than five variegated seeds ever having been found on any one otherwise self-colored ear. But it occurs with considerable regularity, for from one third to two thirds of the ears of some heterozygous or partly heterozygous lots have one or more variegated seeds. In some strains of self-colored maize that have arisen by mutation from variegated strains, no tendency to a reverse mutation has been observed. It seems possible, therefore, that there exist distinct self-color factors which produce identical end results—self color—and which differ in no way except in relative frequency of mutation.

Certainly there exist two, and probably three, distinctly different types of variegated pericarp. The most obvious difference between them is in the amount of red (or brown) color produced. But the fundamental difference is probably only a matter of relative frequency of

factorial change. One type is very light variegated, i. e., has little red (or brown) color—few more or less fully self-colored seeds and few even that are prominently striped with color—because the factor concerned changes to a factor for self color comparatively rarely. Medium variegated types have more self-colored seeds and more seeds with prominent stripes of color because in them the factorial change occurs more frequently. In very dark variegated maize (a type little studied as yet) the same change takes place with still greater frequency.

In all types of variegated pericarp, ears with all or nearly all seeds self-colored or near self are less common than ears with small patches of near self seeds. Ears of the latter sort are less common than those with scattered near self seeds. Near self seeds are less commonly seen than half self and the latter less commonly than seeds with broad self-colored stripes. Most common of all are narrow streaks of color. Practically all seeds of medium variegated ears have numerous streaks of that kind. Even the lightest variegated ears have some seeds so marked. All this, I am inclined to believe—although perhaps there is not sufficient evidence to substantiate it—is because the factorial change occurs with increasing frequency in the later stages of ontogeny. If this is true, the several types of variegated pericarp differ in frequency of factorial change by virtue of the fact that the change begins earlier in some types than in others. On this basis colorless seeds of very light variegated ears might be regarded as the extreme of delayed factorial change, for such seeds produce variegated ears rather than colorless ones in later generations.

According to this interpretation, then, there are, in this somewhat remarkable series of multiple allelomorphs, many degrees of factorial constancy. On the one extreme are self-colored and colorless races, both as constant probably as most Mendelian characters. Next to these are the self-colored types that exhibit from one to four or five variegated or partially variegated seeds on perhaps a majority of the heterozygous ears. Then comes the very light variegated type in which a factorial change to self color comparatively rarely occurs at a sufficiently early stage in ontogeny to affect the germ cells but somewhat more frequently at later stages. At the other extreme is a little known type of very dark variegation in which the factorial change occurs so frequently that all ears, so far as observed, have numerous self-colored or near self seeds. Medium variegated races—probably of more than one type—occupy an intermediate place in the series.

There can be no question that at least the more distinct types of

variegated pericarp are inherited in a simple Mendelian way. They segregate out sharply and apparently without contamination. While the factorial changes described are doubtless non-Mendelian, they are in no sense anti-Mendelian. Genetic modifications are not the concern of Mendelism but of mutation. The essential feature of Mendelism is the segregation of unit factors without their contamination. There is a tendency on the part of some to add as another essential the absolute constancy of unit factors. Doubtless most geneticists who have dealt at first hand with Mendelian phenomena regard unit factors as relatively stable. Few presumably, who have studied pedigree cultures extensively, would hesitate, however, to admit the possibility of an occasional rare mutation. If any unit factor may possibly be modified once, may not others change many times? Much recent work, connecting genetical behavior with the cytological phenomena of reproduction, affords convincing evidence that unit factors are, or have their basis in, material substances. Nothing is better known than that specific, even though closely related, organic compounds differ remarkably in their stability. It seems reasonable, therefore, that specific unit factors might differ widely in constancy. But, whether reasonable or not, they appear in fact so to differ.

Perhaps it is too early to venture further in what may prove to be only fanciful speculation. Whether or not, however, the interpretation here suggested is finally accepted, it will best serve its purpose as a tentative hypothesis if it is boldly followed in whatever way it seems to point. With this as justification, then, it is suggested that some of the divergent results of selection within pure lines, or what pass for pure lines, and in clonal populations may find a rational explanation in accordance with the hypothesis developed in this paper. There seems abundant evidence that selection involving several variable characters within pure lines of the common cereals, for instance, has no effect. On the other hand, unpublished results obtained by WEBBER and MYERS leave little room for doubt that selection is often times effective within tuber-lines of the common potato. It does not seem unreasonable to expect many gradations from organisms, in which on the one hand, particular characters respond somewhat readily to pure-line selection, to organisms with which, on the other hand, it will be impossible to demonstrate any such effect.

In view of the foregoing suggestions and in order that there may be no misunderstanding of my position, it may be well to add that I see no reason for abandoning the pure-line concept which has played so

important a part in the clarification of our ideas of inheritance. While we shall have to recognize that it has limitations, there is little in this study to indicate even a lessening of its importance. Even though factorial modification occurs frequently, it can have little influence upon the trend of evolution, if, as in variegated pericarp of maize, it is merely the same modification occurring again and again, and that modification being subject to occasional reversal. Much less is there anything either in the facts here presented or in the speculations concerning them to justify positive assertions of inconstancy of unit factors when the material employed is of questionable purity or when it has not been subjected to careful factorial analysis.

SUMMARY

Distinct variations in variegated ears of maize are described. Results previously reported have been confirmed with more favorable material and new phases of the problem have been investigated. The seed ears used in the later studies have all been pollinated by colorless strains to avoid difficulties arising from the uncertainty of the purity of the pollen of variegated races. Self-colored, partly self-colored, variously variegated and colorless seeds from variegated parent ears, thus pollinated, have given progenies containing a percentage of self-colored ears roughly proportional to the amount of self color in the seeds planted, the maximum being approximately 50 percent from self-colored and near self seeds and the minimum none from colorless seeds. This has been equally true whether the parent ears have been homozygous or heterozygous for pericarp color. In the latter case, the self-colored ears have always occurred at the expense of variegated ears, never at the expense of colorless ones. Medium variegation has been found to be a simple Mendelian dominant to very light variegation. Self-colored ears appearing in the progeny of F_1 ears of this cross have occurred at the expense of medium variegated ears rather than in the place of very light variegated ones. These facts are held to indicate that a genetical factor for variegation mutates to a factor for self color, that only one of the duplex factors ordinarily so mutates, and that the factor for medium variegation mutates much more frequently than that for very light variegation.

Some evidence has been found to indicate the inheritance of a light type of variegation arising as a sporophytic variation on medium variegated ears, but the matter has not been fully investigated. Sufficient evidence has been obtained to warrant the statement that a sporophytic change in type of variegation, resulting in seeds with strongly colored

crown spots associated with self-colored cob glumes, is not inherited as regards either pericarp or glume color.

In a number of cultures of self-colored maize all descended from two presumably unrelated variegated ears, from one to five wholly or partly variegated seeds per ear have occurred on about two thirds of the otherwise fully self-colored ears. Other related and unrelated cultures have not exhibited such exceptional seeds. No variegated seed has, so far as known, ever occurred on a homozygous self-colored ear. A single test has indicated the inheritance of these presumably reverse mutations from self color to variegation, but the question requires further study.

A preliminary histological examination of the developing maize ovary and glumes and of the mature seed has suggested a possible explanation for the peculiarities of coloration of distinct somatic variations and for the inheritance of some of them and non-inheritance of others. The change from variegated to near self seeds associated with little change in color of the glumes is thought to occur only in sub-epidermal cells and for this reason to stand a chance of being inherited, while the change from variegated to dark-crown variegated seeds accompanied by self-colored glumes is believed to be limited to the epidermal layers and hence to be incapable of inheritance.

It is thought that these results favor the idea that single allelomorphs, rather than two or more closely linked factors, are responsible for the color pattern of both glumes and pericarp.

The phenomena studied are held to have an important bearing on the question of unit-factor constancy. The existence of the series of at least nine or ten multiple allelomorphs to which variegation belongs, indicates that a factor for pericarp color has mutated several times. Some of the factors of this series have not been observed to mutate, while others have mutated rarely and still others many times. In fact, the principal difference between certain of the factors is thought to lie in their relative frequencies of mutation. It is suggested that data such as is here presented may help to explain the somewhat diverse results of selection experiments within pure lines, clonal lines, and the like.

LITERATURE CITED

- CORRENS, C., 1910 Der Übergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftblühenden *Mirabilis*-Sippen. Ber. deutsch. bot. Gesell. **28**: 418-434.
- DE VRIES, H., 1905 Species and varieties: their origin by mutation. 2nd Ed., pp. xviii + 847. Chicago: Open Court Pub. Co.

- EAST, E. M., and HAYES, H. K., 1911 Inheritance in maize. *Bul. Conn. Agr. Expt. Sta.* 167. 142 pp.
- EMERSON, R. A., 1911 Genetic correlation and spurious allelomorphism in maize. *Ann. Rept. Nebr. Agr. Expt. Sta.* 24:59-90.
- 1913 The simultaneous modification of distinct Mendelian factors. *Amer. Nat.* 47:633-636.
- 1914 The inheritance of a recurring somatic variation in variegated ears of maize. *Research Bul. Nebr. Agr. Expt. Sta.* 4:1-35. *Amer. Nat.* 48:87-115.
- HARTLEY, C. P., 1902. The improvement of corn by seed selection. *Yearbook U. S. D. A.*, pp. 543-544.
- MORGAN, T. H., STURTEVANT, A. H., MULLER, H. J., and BRIDGES, C. B., 1915 The mechanism of Mendelian heredity. pp. 262. New York: Henry Holt & Co.
- TRUE, R. H., 1893 On the development of the caryopsis. *Bot. Gaz.* 18:212-226.